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REGIONAL DIFFERENCES IN THE DISTRIBUTION OF THE PYRALID MOTH *URESIPHITA REVERSALIS* (GUENÉE) ON FRENCH BROOM, AN INTRODUCED WEED

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Abstract.—The factors influencing the distribution of the moth *Uresiphita reversalis* (Guenée) on French broom, *Genista monspessulana* (L.), its major host plant in California, were investigated. Within an intensively searched 7000 km² area around the San Francisco Bay, larvae were abundant on broom in the region east of the Bay, but consistently absent northwest of the Bay. In field experiments there were no differences in egg mortality, larval development, pupal weight, predation, plant chemistry, average ambient temperatures or solar radiation between the two regions which might account for the distribution of the insect. Survivorship of experimentally placed larvae was dramatically reduced in field sites northwest of the Bay compared to sites east of the Bay during a rainy winter season. Winter precipitation was consistently twice as high northwest of the Bay compared to east of the Bay, and large losses of larvae were associated with rainfall. After three years of drought in California, larvae were found in a site northwest of the Bay for the first time. It is postulated that heavy rain is a major source of mortality for these insects, which, along with other unknown factors, may preclude establishment in particular microclimates.

Key Words.—Insect distribution, *Uresiphita*, Pyralidae, *Genista*, *Cytisus*, precipitation

French broom, *Genista* (= *Cytisus*) *monspessulana* (L.), is a naturalized leguminous shrub, native to the Mediterranean, and is well adapted to the climate of coastal California, where it was introduced about 100 years ago. It has since become an important weed in parts of the state. Its only major herbivore in California, *Uresiphita reversalis* (Guenée) (Lepidoptera: Pyralidae), was first reported in large numbers in California on *Genista* and "other brooms" (Keifer 1931) in Ventura and San Diego Counties in the southern part of the state. According to California Department of Food and Agriculture (CDFA) records, in 1958 the distribution of *U. reversalis* remained limited to the southern counties.

The earliest records of *U. reversalis* from northern California are from the early 1980s (J. Powell, pers. comm.). The larvae are aposematic and restricted to a few genera of the Leguminosae containing quinolizidine alkaloids, e.g., *Genista, Lupinus* and *Laburnum* in California (Bernays & Montllor 1989). Larvae are known to have been deliberately released (S. Bunnell, pers. comm) in the San Francisco Bay area, but the insect has become established only in selected regions. For example, in 1986, it was conspicuously rare northwest of the Bay, where the plant is very abundant and rapidly spreading, in spite of multiple releases dating back to 1975. In nearby areas across the Bay to the east, however, *U. reversalis* was commonly found defoliating French broom, completing several generations per year on this host (Bernays & Montllor 1989).

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In this study, we have chosen a fairly recent association between an introduced weed and its primary herbivore to study factors which might account for the highly disjunct distribution of the herbivore on a relatively small scale (within a 7000 km^2 area). The factors examined in areas where insects were present or absent were 1) egg and larval mortality with or without predators excluded, 2) larval development and pupal weight, 3) weather, specifically temperature, solar radiation, and precipitation, and 4) plant characteristics, specifically nutrients and relevant secondary compounds, which are known to influence the feeding of this species (Montllor et al. 1990).

METHODS AND MATERIALS

Surveys.—Surveys were undertaken around the San Francisco Bay Area during the summer and fall of 1986–1988, to quantify the apparent differences in distribution of *G. monspessulana* and *U. reversalis.* The insects are multivoltine and non-diapausing. They build up during the first half of the year and reach peak abundance in September–October. On visits to different regions, stops were made on roads and paths, concentrating on sites where there was a possibility of finding the plant. Overall coverage of representative parts of approximately 7000 km^2 around the San Francisco Bay was attempted, excluding dense urban or industrial regions. Areas of up to 10,000 m^2 at each of 90 sites around the Bay area were thoroughly searched for plants. The plant is most common along roadsides and is easily identified in transit, but absence in sites was checked by additional searches. Where the plant was found, thorough searches for insects or insect damage was made on at least 50 plants/site unless fewer plants were present.

Development of a Natural Population of U. reversalis.—A population of *U. reversalis* was followed over a year to better understand its phenology. A 500 m roadside transect of broom in Oakland, Alameda Co., was surveyed weekly (or sometimes bimonthly in winter) from 14 Dec 1988 to 8 Feb 1990. Each week the same 100 bushes, usually 2 m apart, were examined for eggs and larvae, and the numbers and instars were noted. Plants were approximately 1–2 m high at the start of the survey.

Releases.—In order to obtain empirical evidence relating to the suitability of San Francisco Bay area regions for *U. reversalis,* larvae were released in specific sites over several years, and sites were subsequently searched for establishment (Fig. 1). Prior to our experiments, larvae had been released in the Bay Area in 1975 in Alameda Co., east of the Bay (referred to hereafter as EBay) (two sites, approximately 50 larvae per site) and in Marin Co., northwest of the Bay (hereafter referred to as NWBay) (two sites, approximately 50 and 1000 larvae) (S. Bunnell, pers. comm.). In 1985–86, no wild populations of *U. reversalis* were known from NWBay sites, while insects were abundant throughout the EBay. Subsequently, we released larvae in the NWBay at Sky Oaks in September 1985 (100 late instars); April 1986 (1000–1300 late instars); and July 1986 (400–500 late instars). In April, June, July, September and November 1988, between 200 and 375 eggs or first instar larvae were released on each occasion in three NWBay sites as part of our field experiments (see below). One of these field sites (Olema) was checked for evidence of larvae monthly from June–October 1989. The other two (Sky Oaks and Muir Woods) were intensively searched for larvae in October 1989. At

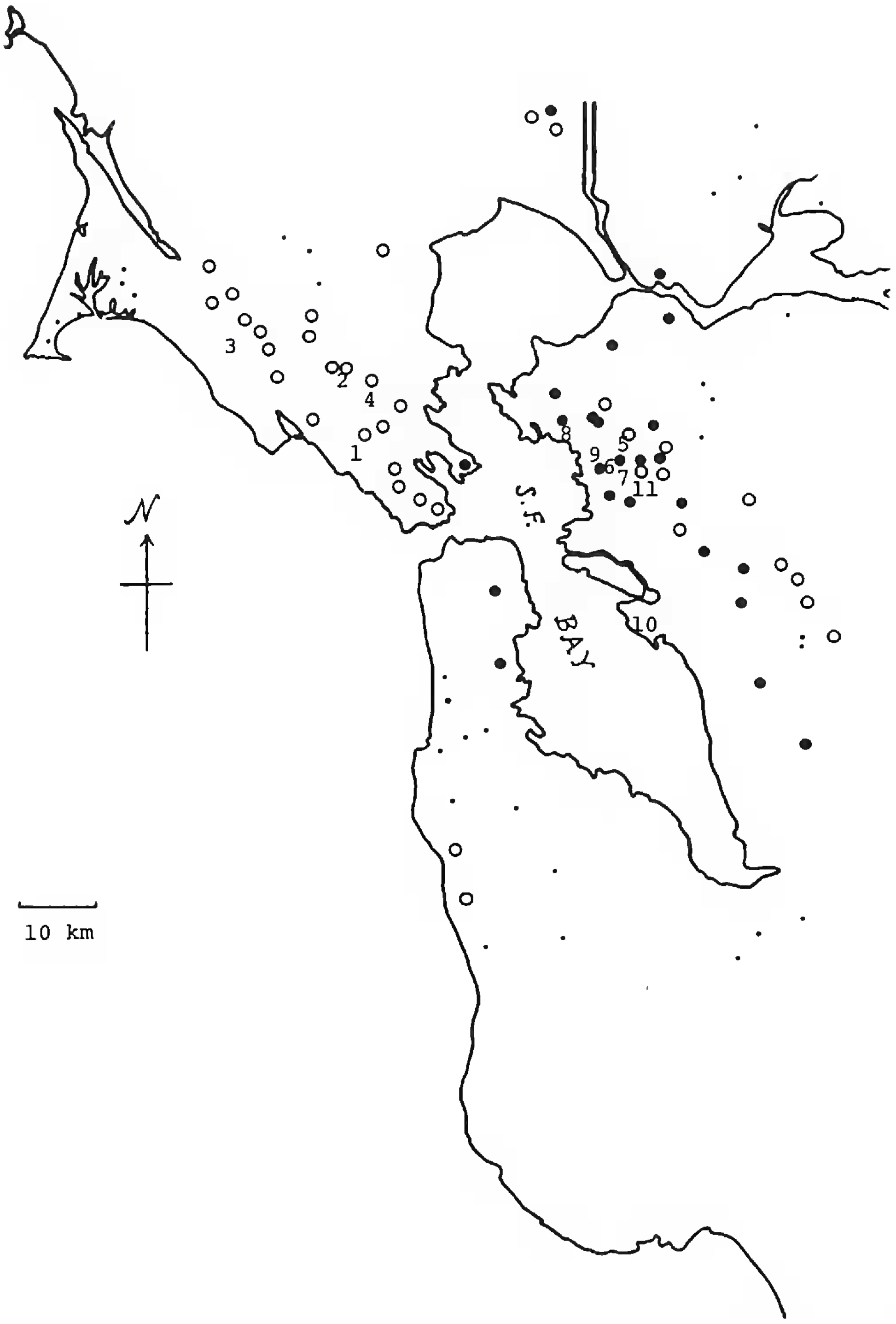

Figure 1. Results of surveys around the San Francisco Bay Area for the presence of *Genista monspessulana* and the pyralid folivore *Uresiphita reversalis*. Solid circles = plant and insect both present; small dots = both absent; open circles = plant present, insect absent. Experimental (E) and weather measurement (W) sites in Northwest Bay and East Bay regions: NWBAY 1, Muir Woods (E, W); NWBAY 2, Sky Oaks (E, W); NWBAY 3, Olema (E); NWBAY 4, Kentfield (W); EBAY 5, Claremont (E); EBAY 6, LHS (E); EBAY 7, Mt. View (E); EBAY 8, Gill Tract (W); EBAY 9, Berkeley (E, W); EBAY 10, Oakland Airport (W); EBAY 11, Oakland—natural population development.

each site, an area of approximately 5000 m^2 around the place of release was intensively searched.

Field Experiments.—Field sites were chosen in Alameda and Marin Counties, east (EBay) and northwest (NWBay) of the San Francisco Bay, respectively. Larvae of *U. reversalis* had previously been observed feeding on French broom at or near all the EBay sites, but at none of the NWBay sites; these sites represented areas where this species was abundant, and rare or absent, respectively (Fig. 1). A total of four different sites were used over the course of experiments in the EBay, and three in the NWBay.

Egg Survival.—A possible difference in field survival of eggs in the two regions was experimentaly investigated. Egg masses of *U. reversalis,* deposited on broom in a laboratory culture (Bernays & Montllor 1989), were used for examination of pre-hatching mortality. The eggs were counted and placed in the field by pinning the leaves on which the eggs had been deposited onto 3–5 plants at each of three EBay and NWBay sites, on five different occasions. Each plant received one or more egg masses, consisting of approximately 30 eggs (range = 13 to 68). A total of 71 and 72 egg masses were placed at NWBay and EBay sites, respectively, over a year: in June, July and August 1988, and April and June 1989.

Pinned leaves were collected four to five days after eggs were put out, and examined under a dissecting microsope for signs of non-hatching, hatching, and/or predation of eggs. Predation was assumed to have occurred when eggs and their shells were gone from the leaf surface, or when a portion of the leaf containing eggs had been chewed off. No egg parasites are known for this species in California.

Larval Survival and Development.—To examine possible differences in larval survival in the two regions, eggs (Experiment 1) or first instars (Experiments 2–5) from a laboratory culture, were laid or placed on single leaves of broom in groups of approximately 25 (range = 21–35), and pinned to bushes in the field. Three to four plants 1–2 m tall at each of three EBay and NWBay sites were selected. Two groups of neonate larvae, or ready-to-hatch eggs, were placed on each plant, one enclosed in a white nylon mesh bag to exclude natural enemies, and the other left uncovered. Positions on plants were representative of those found naturally. Insects were put out on five occasions, starting in April, June, July, September, and November 1988. Larvae were counted at intervals until all insects in bags had pupated and all larvae in the open had disappeared (larvae leave the plant to pupate). Because large larvae will move to adjacent branches on the same or a neighboring plant to feed, isolated bushes were used if possible. Otherwise, the neighboring bushes were always searched for missing larvae. Survivorship in the open and in bags was estimated by counting remaining larvae twice during the experiments. For Experiment 5 (November) no larvae were enclosed in bags. Pupae from bags from Experiments 3 and 4 were counted and weighed in the laboratory.

Because late fall and winter mortality appeared to be important, additional simplified experiments were carried out in the winter of 1989–90 at one EBay and one NWBay site. In these, 10 to 15 second instar larvae were placed on each of 7–10 plants per site in November (Experiment 6, starting $n = 110$ larvae) and in January (Experiment 7, starting $n = 100$), and remaining larvae were counted weekly.

Two measurements of development were made during four of the experiments in which larvae were placed in the field. The distribution of instars in bagged and unbagged (open) cohorts at all sites at a given sampling date was determined. Sampling dates ranged from 13 to 24 days after the beginning of a given experiment. Sampling of all sites was always accomplished within one or two days.

Plant Chemistry.—The possibility that regional differences (genetic or environmental) in plant chemistry might affect insect abundance was also examined. Plant material was collected from experimental plants at all sites during the second (June 1988) larval survival experiment.

Material was collected twice, early and late in the experiment, dried in an oven at 70° C, and analyzed for total alkaloids (Montllor et al. 1990), Kjeldhal nitrogen, and soluble carbohydrates (anthrone method). Nitrogen and carbohydrates were selected as the major important nutrients. Quinolizidine alkaloids were selected as the characteristic secondary components of the host plant. These are phagostimulants for *U. reversalis* larvae, and are sequestered by them (Montllor et al. 1990). We have also found that the sequestered alkaloids are effective deterrents to hymenopteran predators of these larvae (Montllor et al. 1991).

Weather.—Because there appear to be marked regional differences in the weather around the San Francisco Bay Area, the possibility that climatic factors may be correlated with insect abundance was examined. Temperatures, precipitation and solar radiation were collected with a LICOR datalogger, hygrothermographs, and/or from National Oceanographic and Atmospheric Administration (NOAA) records. Data were collected for three EBay sites and three NWBay sites, at or near the field sites (see Fig. 1). NWBay weather sites were Muir Woods (at a field site), Sky Oaks (at a field site), and Kentfield (4.5 km from Sky Oaks field site). EBay sites were Berkeley (1–2 km from LHS, Claremont, Dwight-Derby field sites), Gill Tract (5–8 km from all sites excluding Mt. View), and Oakland (4.5 km from Mt. View field site).

Laboratory experiments.—Daily temperatures fluctuated more widely in NWBay sites than in EBay sites, so we examined the effects of temperature fluctuations on larval mortality. Some larval Lepidoptera apparently survive better under fluctuating, rather than constant, temperatures in the laboratory (McDonald 1990). However, infectious agents may be more virulent at alternating than at constant temperatures, e.g., *Bacillus popillae* in certain scarab beetles (Milner et al. 1980).

Insects were reared at two temperature regimes in environmental chambers in the laboratory, in which the mean temperature was the same, but one fluctuated and the other did not. Five groups of 10 first or second instar larvae were placed on cut broom at temperatures of either 32°:8° C (12L:12D) or at 21° C (±1°) (12L:12D). Food was changed and larvae were counted every other day until larvae began to pupate. This experiment was replicated three times for a total of 150 larvae per treatment.

RESULTS

Surveys.—General surveys for *G. monspessulana* around the San Francisco Bay area demonstrated that the plant was abundant northwest of the Bay, and was also common east of the Bay. Fewer plants occured on the San Francisco peninsula, and south of San Francisco natural vegetation predominated, with less apparent invasion of this weed (Fig. 1). Populations of *U. reversalis* were common on broom east of the Bay but mostly absent on the west side of the Bay. Most sampling was done at times when insect populations would be at or near their peaks. The scarcity of this insect northwest of the Bay, and its absence on the northwest coast, where broom populations were large and spreading, was striking.

In a subsequent survey of NWBay field sites, larvae of *U. reversalis* were found at Sky Oaks in October 1989. Searches of Olema and Muir Woods, our two other NWBay sites found no *U. reversalis* in 1989. The last releases at all these sites had been in November 1988 (Experiment 5), therefore populations apparently successfully overwintered at Sky Oaks in 1988–89 for the first time.

Development of a Natural Population of U. reversalis.—In 1989, at the Oakland (Alameda Co., EBay) site selected to follow a natural population, larvae were

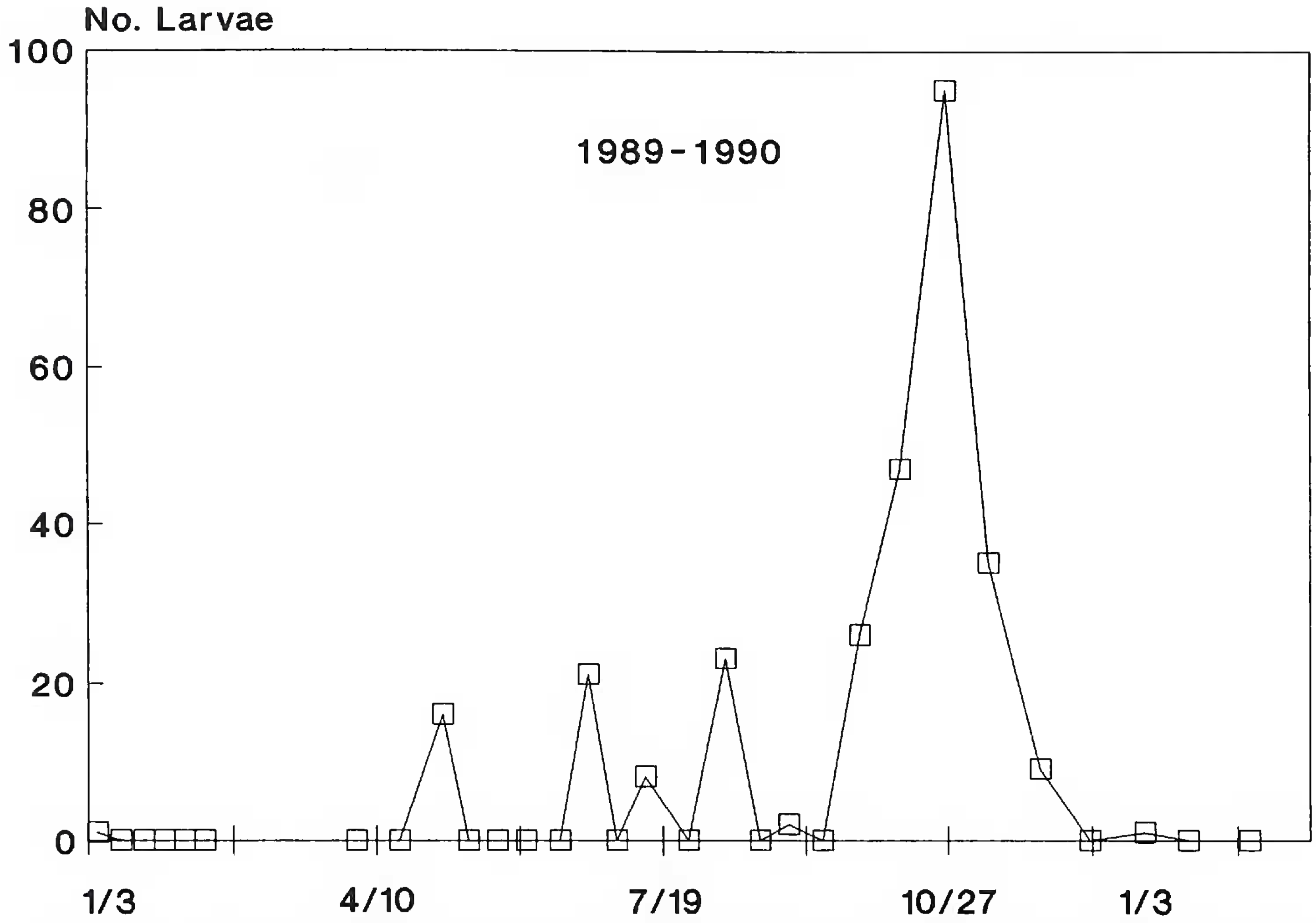

Figure 2. Number of second instar larvae of *U. reversalis* on 100 plants of *G. monspessulana* (site 11) at given sample dates over an entire year (1989).

found in all months, but numbers were very low in January through March. Over four years, adults were caught at light traps in neighboring Berkeley in all months except January (J. Powell, pers. comm.), and the first new generation of caterpillars appeared at our site in April. Numbers built up slowly through the summer, reaching a peak in October.

Numbers of second instars peaked at intervals of 47 to 77 days, beginning in May (Fig. 2) (eggs and first instars are inconspicuous, therefore their presence/absence is not reliably recorded). The first peak occurred on 5 May, a second 51 days later (23 Jun), another 47 days later (10 Aug), and the last and biggest 77 days later (26 Oct). It is not certain that each new peak represents a new generation, since in laboratory studies, insects reared at an average temperature of 17° C (a realistic temperature for this site in spring/summer; see Table 3) took a mean of 76 days to develop from egg to adult (Montllor et al., unpub.). However, depending on insolation these caterpillars may increase their body temperature by 3° C or more at this air temperature (Bernays & Barbehenn, unpublished data). Adult emergence in the spring may be somewhat staggered depending on pupation microsites, but it is likely that there are 3–4 generations during the year.

Field Experiments.—Field experiments, in which eggs or young larvae were placed at selected sites, covered the period from April through November, months during which young larvae were found in our natural field population (Fig. 2).

Instances of egg predation were more frequent in NWBay sites on four out of five occasions. A total of 34% of the egg masses showed some evidence of predation in NWBay sites (n = 71), compared to 19% in EBay sites (n = 72), but in spite

Table 1. Survivorship of larvae when placed as neonates (or eggs) on open branches of broom in EBay and NWBay sites (1988). Starting numbers of larvae were between 200 and 375 for each experiment, placed on 3–5 plants at each of three sites in each region.

			% survivorship		
Exp. (start)	Days from start	Instar	EBay	NWBay	P*
1 (April)	11–12	2–3	36	42	>0.1
	22–23	3–5	10	12	>0.4
2 (June)	7–8	2–3	50	40	<0.03
	17–19	2–5	21	20	>0.8
3 (July)	8	3–4	37	42	>0.1
	23	3–5	24	21	>0.5
4 (Sept.)	12–13	2–3	20	21	>0.8
	21–22	3–4	9	10	>0.7
5 (Nov.)	11–12	2	35	20	<0.001
	20–21	2	25	12	<0.001

* Numbers of living and dead (or missing) larvae compared between regions by Chi-square test.

of this trend, there was considerable variation and the difference between regions was not significant ($P > 0.05$, G-test). There were no differences in hatching rate, and no parasitism.

Numbers of larvae remaining on the bush on which they had been originally placed (or on an adjacent bush) was used as our measure of larval survivorship. Survival of larvae up to approximately the fourth instar on open (unbagged) branches of broom was significantly greater in EBay sites in two of the five experiments; in the experiment conducted during the 1988–89 winter rainy season this difference was large and sustained (Table 1). However, during the winter of 1989–90, no difference in survivorship of larvae put out as second instars (Experiments 6 and 7) was found between a NWBay site (Sky Oaks) and an EBay site (Mt. View). This may be, in part, because little rain fell in either area during those experiments (see Weather below).

The number of insects surviving to pupate on bagged branches (i.e., predators excluded) was significantly greater in EBay sites in two of the four experiments (June and July) in which larvae were bagged ($P < 0.05$, Mann-Whitney U-tests); there was no significant difference in the other two experiments. Overall, the mean survival to pupation was 28% in EBay sites compared to 17% in the NWBay sites ($P < 0.03$, ANOVA) over the four experiments. Survival in bags was usually lower in NWBay compared to EBay sites, though the pattern over the four field experiments was inconsistent (Fig. 3). The greater mortality in bags at NWBay sites is evidently responsible for the difference in survival to the pupal stage (only measured in bags) between regions. The reason for this difference is not known.

Survival of larvae in bags was greatly increased compared to that of unprotected larvae in both areas. In NWBay sites, survival in the open was 56% of that in bags; in EBay sites survival in the open was 48% of that in bags. Although larvae of *U. reversalis* are not preferred by many arthropod predators in laboratory studies (Montllor et al. 1991, and unpublished), they are subject to predation by Hemiptera (Anthocoridae) and Hymenoptera (Vespidae) in the field (Bernays & Montllor 1989). However, predation pressure, measured as the difference between survival

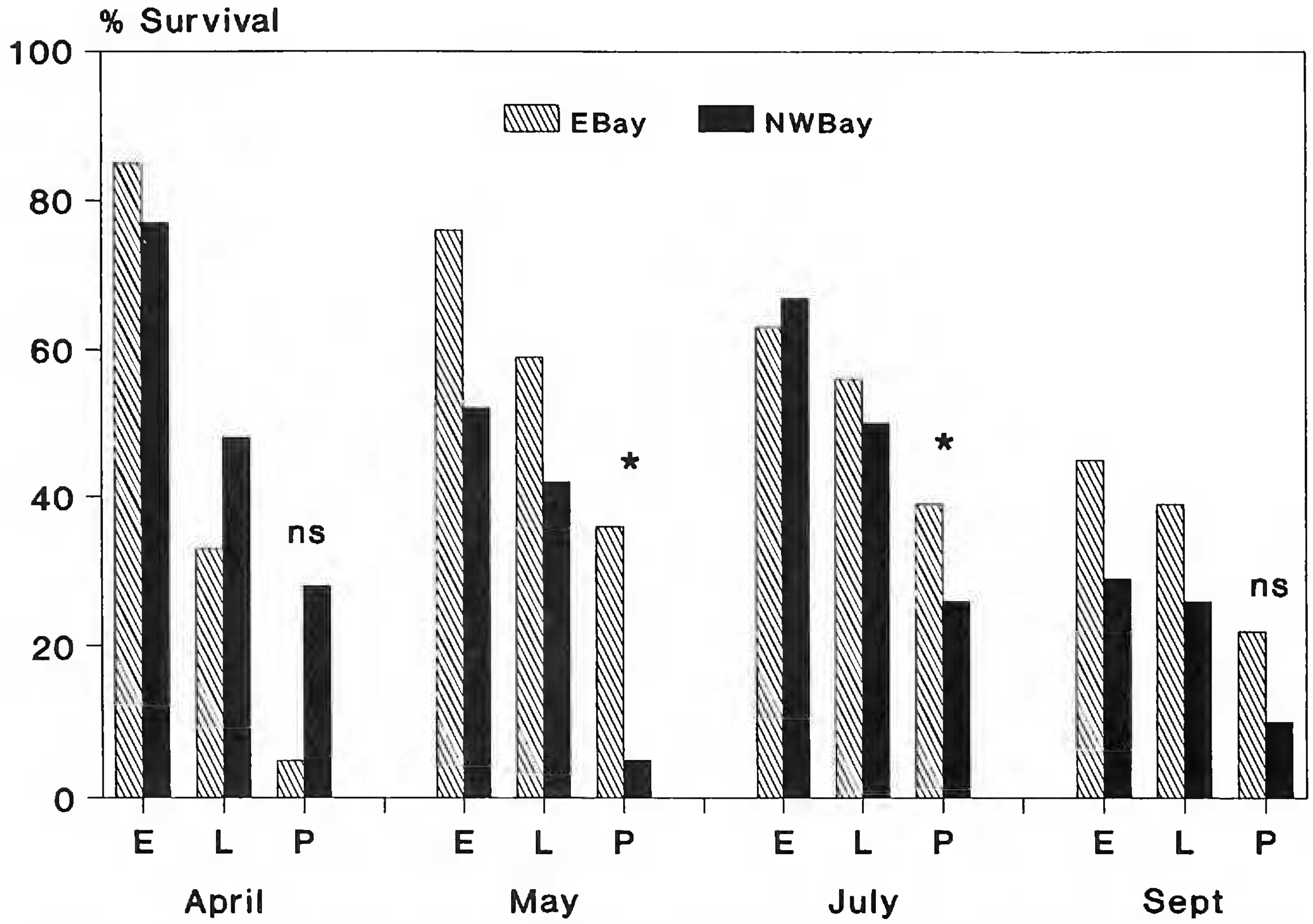

Figure 3. Percent survival of *U. reversalis* cohorts bagged on *G. monspessulana* in four experiments in 1988 at EBay and NWBay sites (pooled). Insects were censused three times: E = early (instars 2–3); L = late (instars 3–5); P = pupae. *Numbers of pupae significantly different between regions ($P <$ 0.05, Mann-Whitney *U*-test); ns, not significant.

on open compared to bagged branches, was not demonstrably different between the two areas under study here.

Development.—Distributions of larval instars were significantly different, but inconsistently so, in EBay sites compared to NWBay sites in all experiments. Larvae put out in April and June (Experiments 1 and 2) developed more quickly in the EBay sites. Although a greater proportion of larvae put out in July (Experiment 3) had reached the fourth instar after two weeks in NWBay compared to EBay sites, there were also more early instars in NWBay sites (on open branches, 11% were still second instars, compared to none in EBay sites). In contrast to the earlier season results, larvae put out in September were ahead in NWBay sites after 22 days (Fig. 4). Age structure of larvae in bags and in the open showed similar differences, indicating that where differences occur between regions, they are not likely to be due to differential loss of early instars to predation, or late instars to disease. In sum, during our experiments, *U. reversalis* larvae appeared to have an early season advantage in EBay sites, and a late season advantage in NWBay sites, with no net overall effect of region on development rates.

In two experiments, fresh weights of pupae collected in the two regions were compared. In Experiment 3 the mean weights of pupae in EBay sites compared to NWBay sites were 87.8 and 92.5 mg, respectively ($P > 0.6$, nested ANOVA). Similarly, in Experiment 4 mean pupal weights were 91.1 and 98.4 mg in EBay compared to NWBay sites ($P > 0.6$, nested ANOVA). In both experiments, there

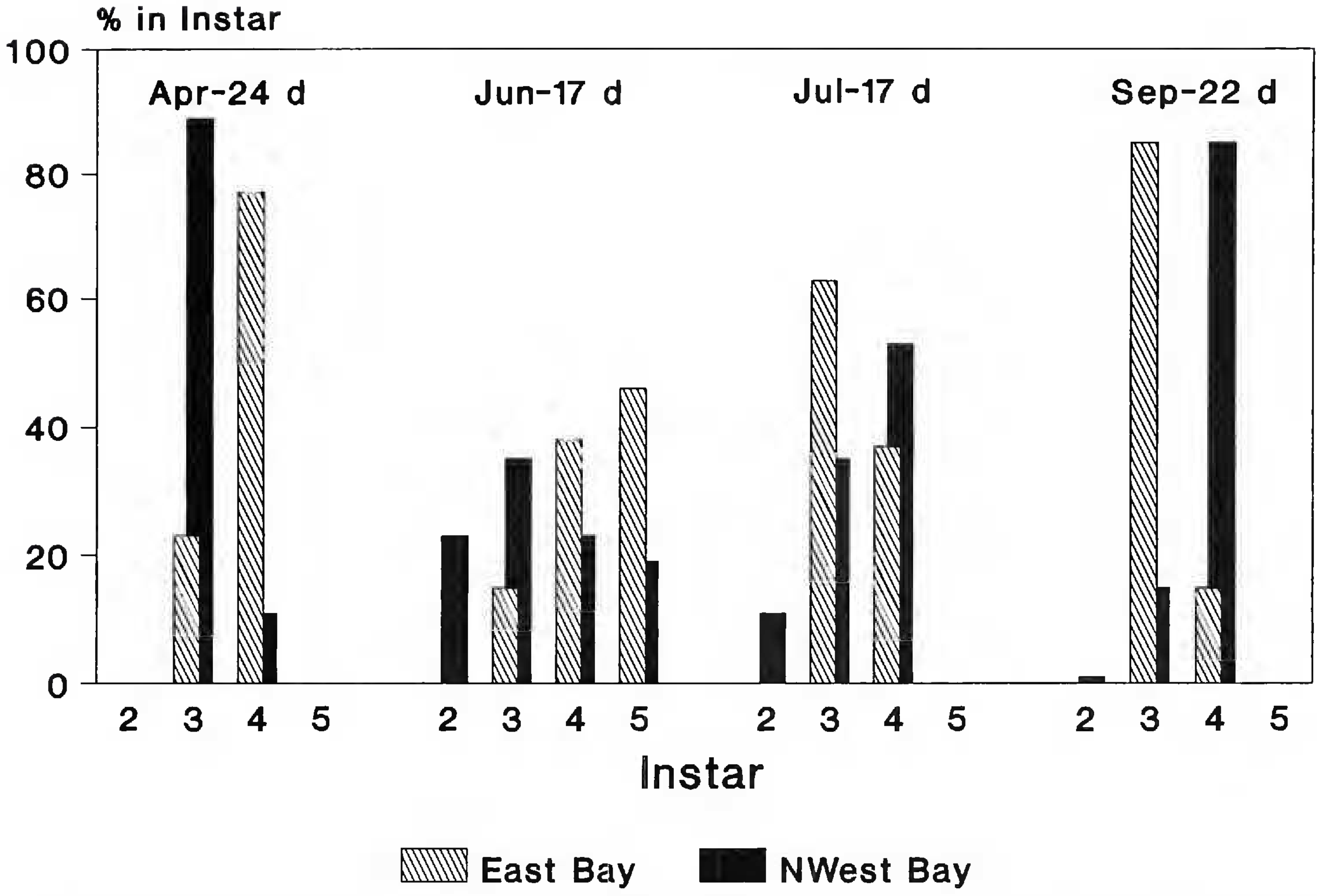

Figure 4. Percent of larvae which were given instars on open branches during four experiments, beginning in given months. Sampling dates were given number of days (d) after putting out 1st instar larvae (or eggs, in April). All distributions were significantly different between regions ($P < .001$, Chi-square).

was significant variation in pupal weights between sites within regions but not between regions.

Plant Chemistry.—No differences in soluble carbohydrates, total nitrogen, or total quinolizidine alkaloids were found between plants at the NWBay and EBay sites (Table 2).

Weather.—Rainfall was consistently higher in the NWBay in 1985-1989 (Fig. 5). Data collected from other sites and from NOAA corroborates this difference both during years of drought (1986–91) and of normal rainfall. NOAA reports "normal rainfall" to be more than twice as great in Kentfield (NWBay) as in Berkeley (EBay) in a typical November, December, January and February. For

Table 2. Mean levels (± SD) of carbohydrates (CHO), Kjeldahl nitrogen (N) and quinolizidine alkaloids (QA) in broom samples (% DW).

Region (no. plants)	CHO	N	QA
EBay (12)	8.4 ± 2.3	2.2 ± 0.3	0.4 ± 0.2
NWBay (8–9)	6.7 ± 0.8	2.2 ± 0.3	0.3 ± 0.3
P (*t*-test)	>0.05	>0.05	>0.05

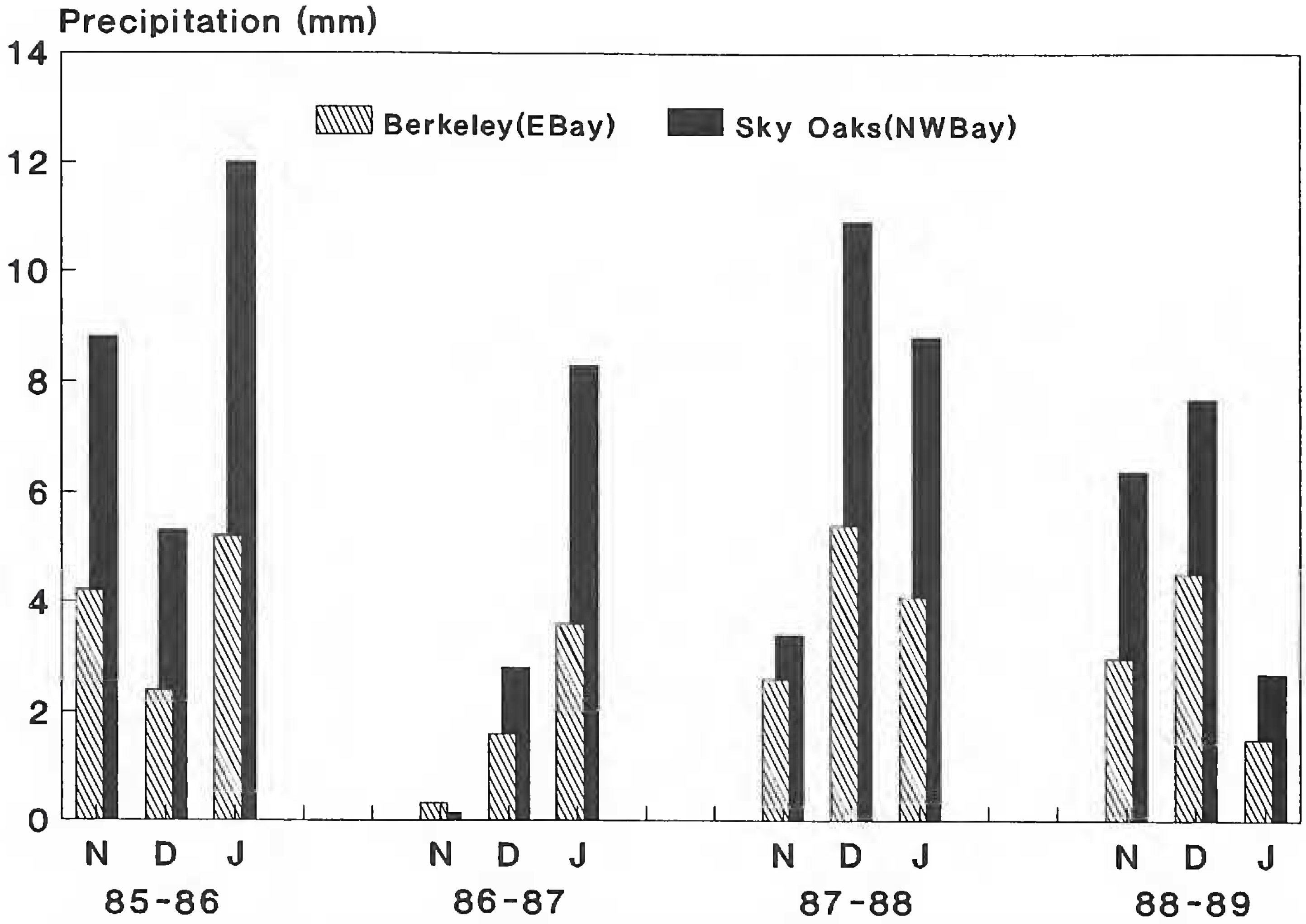

Figure 5. Precipitation during November, December and January in four years at Berkeley (EBay) and Sky Oaks (NWBay).

example, total "normal rainfall" at these locations for these four months are reported as 85 mm and 40 mm, respectively.

Total numbers of larvae at our monitored natural field site in the EBay fell dramatically at the onset of the late fall rains. The relationship between larval mortality and rainfall was examined further by regressing larval losses against precipitation during the first two weeks of Experiments 5, 6 and 7, conducted during the 1988–89 and 1989–90 rainy seasons. This regression showed a significant correlation ($r = 0.67$, $P < 0.04$).

Mean daily temperatures were not significantly different in the two regions in any of the four months sampled in 1988 (Table 3). Although mean daily fluctuations in temperature appeared to be slightly larger in NWBay sites, the differences only approached significance in one month (July; $P = 0.06$).

Solar radiation was compared at Sky Oaks (NWBay) and Berkeley (EBay) over 72 days in May through August 1988. All days for which daily totals for both sites were available were used in the sample. Summer fog can be very common in these areas, but may differ significantly on a microgeographic scale. We found mean total daily radiation at the two sites to be very similar: 7158 Wm^{-2} at Sky Oaks and 7087 Wm^{-2} at Berkeley ($P > 0.3$, Wilcoxon rank sum).

Laboratory Experiments: Temperature Fluctuation.—When the three experiments (each with 50 insects per treatment) were pooled, mortality was not significantly higher for larvae reared in an environment in which temperatures fluctuated widely than at a constant temperature. At 8–32° C, 23% of the larvae died, whereas 15% died when reared at 21–22° C (Chi-square, $P > 0.1$).

Table 3. Temperature measurements (°C, mean ± SD) from three EBay and three NWBay sites during four months in 1988.

	May	Jul	Sep	Dec
A. Monthly means of daily median temperatures (high ± low/2)				
EB	14.7 ± 3.0	18.2 ± 2.6	16.6 ± 1.8	9.5 ± 3.7
NWB	14.6 ± 3.6	19.9 ± 3.5	17.5 ± 3.1	9.8 ± 3.9
P*	0.78	0.39	0.57	0.71
B. Monthly means of daily fluctuation (high–low)				
EB	10.5 ± 4.7	11.2 ± 4.3	11.1 ± 5.2	8.3 ± 3.4
NWB	13.9 ± 5.1	17.1 ± 4.9	15.6 ± 5.5	8.8 ± 3.7
P*	0.23	0.06	0.31	0.78

* Nested ANOVA.

Discussion

Our field experiments showed minimal differences in egg mortality, larval development, pupal weight, predation, plant chemistry, ambient temperatures or solar radiation between the regions where *U. reversalis* was abundant or absent. Early winter mortality was significantly higher for larvae in NWBay sites, and other evidence also suggests that winter precipitaion may be at least one important factor in limiting the distribution of this insect. Other sources of mortality certainly exist, but most remain unexplained (e.g., differences between EBay and NWBay mortality in May and July 1988).

Moran & Whitham (1988) have suggested that weather may have a large and direct effect on insect populations on which predation and parasitism are relatively low. Populations of a leaf mining sawfly, *Schizocerella pilicornis* (Holmgren), are rarely attacked by natural enemies and appear to be limited in distribution in northern California by climatic factors such as temperature and solar radiation (Wrubel 1990). Although predation may account for some losses of *U. reversalis* larvae in summer months (Bernays & Montllor 1989), we did not find differences in predation between areas where *U. reversalis* was common or absent. Larvae are probably protected from many vertebrate and invertebrate predators by virtue of the alkaloids which they sequester from *Genista* (Montllor et al. 1990, 1991). In our experience with field collected larvae, parasitism is also relatively rare, with the exception of a tachinid pupal parasite. Therefore there is a potential for large direct or indirect effects of weather on populations of this insect.

Although we have not found differences in temperature or solar radiation in our two regions under study, precipitation, which is much greater northwest of the Bay than east, may play an important role in larval and pupal mortality. The major causes of pupal mortality are not known. However, large losses of larvae were clearly related to rainfall during our experiments and in the natural population of *U. reversalis* which we sampled regularly for over a year. Observations of other wild populations of *U. reversalis* in the East Bay showed that on four occasions during 1985–86, population losses of 80% or more were recorded in association with heavy rains. In one case, 14 larvae were counted the day before a heavy storm; the following day, 2 larvae remained on the same bushes (Bernays, unpublished).

Although *U. reversalis* larvae were released at Sky Oaks in 1985–1988, only in the fall of 1989 were new generations found there; in previous years, insects presumably failed to overwinter, as new larvae were never found. That winter (1988–89) was the third of below-normal rainfall in northern California. No larvae were found in fall 1989 at the other NWBay sites where field experiments had been carried out the previous two years.

The probability of establishment of a field population even under the best environmental circumstances is not known. Probability of establishment may be quite difficult to measure accurately (Harrison 1989) and experiments were not carried out which might have addressed this issue. However, one of the EBay sites, LHS, did not have an endemic population of *U. reversalis* when we began our experiments in 1986, but by the next year, there were large populations there, whereas there were none in NWBay sites after introductions of similar numbers of larvae. This gives some evidence that the numbers of larvae put out in 1986 were large enough to allow for establishment under the proper conditions, although we cannot rule out the possibility that LHS populations were at least partially the result of migrants from nearby areas.

Weather may also affect mortality of larval Lepidoptera indirectly through incidence of disease or of predation/parasitism. Both rainfall and high temperature maxima have been implicated in increased mortality from granulosis virus of *Pieris rapae* L. (Lepidoptera) larvae (Harcourt 1966). *Bacillus popillae* was shown to be more infectious in certain scarab beetles under fluctuating compared to constant temperatures (Milner et al. 1980).

Although the incidence of disease was not quantified in this study, many flaccid dead larvae were found at all sites in the first three experiments. Such dead larvae collected on 13 Jul 1988 at two EBay sites contained granulosis virus and *Bacillus cereus* Frankland & Frankland, both common disease agents of larval Lepidoptera. We were unable to significantly increase larval mortality in the laboratory by fluctuating rearing temperature. In a recent review, Benz (1987) discusses the problem of environmental effects on disease outbreaks. There are no general patterns, and even with baculoviruses high temperatures or low temperatures can either induce expression of particular diseases or suppress them.

It appears that we have witnessed a persistent decimation of populations of *U. reversalis* in winter, and subsequent populations which are too small to persist, in a particular region of northern California. Four years of drought, coupled with repeated introductions (the last in January 1990) may have finally allowed populations to take a foothold northwest of the San Francisco Bay. A large population was found at Sky Oaks in October 1990. In the spring of 1990, larvae were also found in Ross, Marin Co., 5 km from our nearest field site (Sky Oaks). Whether populations will persist when winter precipitation levels return to normal has yet to be determined.

The possibility that such small-scale weather patterns might dictate this insect's distribution is plausible, and is analogous to altitudinal restrictions, which may be very sharply delimited. Conditions for adult survival in winter, and factors affecting female fecundity in spring are not known for this species. Price et al. (1990) have recently pointed out the importance of natality on insect population dynamics. Although we have emphasized larval mortality factors in our study, we recognize the potential importance of factors affecting successful adult eclosion, mating and oviposition, which we have not measured here.

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